AN INVESTIGATION OF THE HEREDITARY CHARACTER, WOOLLY, IN THE TOMATO[1]

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INTRODUCTION

A condition of very profuse epidermal hair growth exists in some strains of the cultivated tomato, *Lycopersicon esculentum* Mill. The character originated in a field of tomatoes grown by the Campbell Soup Company of Camden, New Jersey and W. S. Porte (personal communication) obtained a seed sample of a tomato having this character from the New Jersey Agricultural Experiment Station. He called the character "Angora." Later, Young and MacArthur (1947), having obtained the selection from Porte, published a description of the character referring to it as both "woolly leaves" and "woolly." Since that time, the character has generally been referred to as "woolly," not as "woolly leaves." Woolly plants are easily distinguished from nonwoolly plants. Due to the profuse epidermal hair growth, woolly plants appear grayish instead of a normal green color.

Upon selfing woolly plants, a ratio of $\frac{2}{3}$ woolly to $\frac{1}{3}$ nonwoolly plants results. However, when a plant heterozygous for a single gene pair is selfed, either a $\frac{1}{4}$:$\frac{1}{2}$:$\frac{1}{4}$ or a $\frac{3}{4}$:$\frac{1}{4}$ phenotypic ratio would be expected. Therefore, this observed $\frac{2}{3}$:$\frac{1}{3}$ ratio indicates that the woolly character is lethal when homozygous, and any plant manifesting the woolly character is heterozygous. The woolly character is one of the very few semidominant lethal factors known in cultivated plants, and the nature of the lethal action has not been investigated in any of them.

Since the heterozygotes survive, the woolly gene is not a gametic lethal. If the woolly gene were lethal only to eggs or only to sperms, a ratio of $\frac{1}{2}$ woolly plants to $\frac{1}{2}$ nonwoolly plants would be expected upon selfing a woolly plant, instead of the observed $\frac{2}{3}$:$\frac{1}{3}$ ratio. Therefore, the woolly gene is not lethal in either type of gamete. For this reason, it must be assumed that the lethal action of the homozygous woolly condition takes place sometime after fertilization. If this lethal action occurs during embryonic development, then upon examination of zygotes or embryos in fruits from self-pollinated woolly plants one might be able to observe disintegration of approximately 25 percent more zygotes or embryos than in fruits from nonwoolly plants. This would be 25 percent of all zygotes and embryos, which includes those which are normal and those which are disintegrating.

If the lethal action of the homozygous woolly condition affected embryo or endosperm development and, as a consequence also affected seed coat development, then in fruits from self-pollinated woolly plants, one would expect approximately 25 percent fewer normal sized seeds per fruit than in similar fruits from nonwoolly plants; but nearly the same percent germination should be found in the normal sized seeds from both types of fruits. Conversely, if the lethal action did not appreciably affect seed coat development as a consequence of its effect on embryo or endosperm development, then one would expect nearly the same number of normal sized seeds per fruit in both woolly and nonwoolly fruits but approximately 25 percent less germination of the normal sized seeds from fruits of woolly plants.

According to Soost (personal communication), in seeds germinated on moist filter paper the number not germinating corresponded to the number of expected

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homozygous woolly plants. Dissection of the ungerminated seeds showed that all contained well-developed endosperm while embryos were at various stages of development, but all poorly developed. Soost also found some segregating seed lots which produced a few plants which he suspected were homozygous woolly. Generally these plants did not develop much beyond the cotyledonous stage. If these plants were homozygous woolly, then the lethal action of this genotype is not always fully manifest. The seed used by Soost came from W. S. Porte. Soost, therefore, believed that the lethal action of the homozygous woolly character affected the embryo and not the endosperm and that the exact point of lethal action depended on the genetic constitution of the individual embryo.

Young and MacArthur (1947) suggested that this lethal action could be due to a chromosomal deletion. Although this is a possible explanation, there has been no cytological evidence presented to support such an hypothesis. The chromosome to which the woolly locus is assigned has been variously designated: Young and MacArthur (1947) designated it as chromosome L.; Lesley (1937) designated it as chromosome A.; Barton (1950) designated it as chromosome 2. The primary basis for Barton's classification is chromosome length at pachytene, chromosome 2 being the second longest chromosome. Barton (1951) also stated that the nucleolus is attached to the short arm of chromosome 2. According to evidence presented by Lesley (1937), those genes so far assigned to chromosome 2 are all in the long arm. According to a recent chromosome map (Rick and Butler, 1956), the woolly locus is at 48 crossover units, placing it near the midpoint of the long arm of chromosome 2, there having been 77 crossover units determined. Thus search for a deletion would be narrowed to a small region of chromosome 2.

The woolly character has been described as affecting all vegetative plant parts (Rick and Butler, 1956). Since epidermis also covers reproductive parts, one might expect to find the woolly character affecting reproductive parts as well.

In all strains of another species of tomato, *Lycopersicon hirsutum* Humb. and Bonpl., there is also a condition of profuse epidermal hair growth, for which condition the specific name *hirsutum* has been applied. Plants of this species have epidermal hairs which are much longer than those on plants of *L. esculentum*, whether woolly or nonwoolly, as can be seen in figures 21 and 22. If epidermal hair growth in these two species is conditioned by different genes, upon crossing a *L. esculentum* plant with a *L. hirsutum* plant, offspring might result which had the combined epidermal hair growth of both parents and would then be "super-woolly." There is no record of lethal action associated with *L. hirsutum* type hair.

Therefore, five questions are considered here: *1.* Do irregularities in development occur which can be attributed to lethal action of the homozygous woolly condition? *2.* Is there a difference between fruits of woolly and nonwoolly plants in number and germination of normal sized seeds? *3.* Do woolly plants possess a chromosomal deletion? *4.* Are parts other than leaves also woolly? *5.* What kind of hair condition results from a combination of the woolly condition with the hirsute condition?

EXPLANATION OF FIGURES IN PLATE I

1. Embryo sac of type not classified because it could not be determined whether fertilization had occurred. 461×.
2. Collapsed embryo sac. The stage of embryonic development prior to collapse could not be determined. 461×.
3. Embryo sac with a normal zygote and endosperm. Zygote upper left. 461×.
4. Embryo sac with a normal embryo and endosperm. Two-celled embryo stage. Embryo upper left. 461×.
5. Embryo sac with a normal embryo and endosperm. Many celled embryo stage. 461×.
6. Embryo sac with a normal embryo and endosperm. Many celled embryo stage. 461×.
7. Embryo sac with a disintegrating zygote and endosperm. 461×.
8. Embryo sac with a disintegrating zygote and endosperm. 461×.

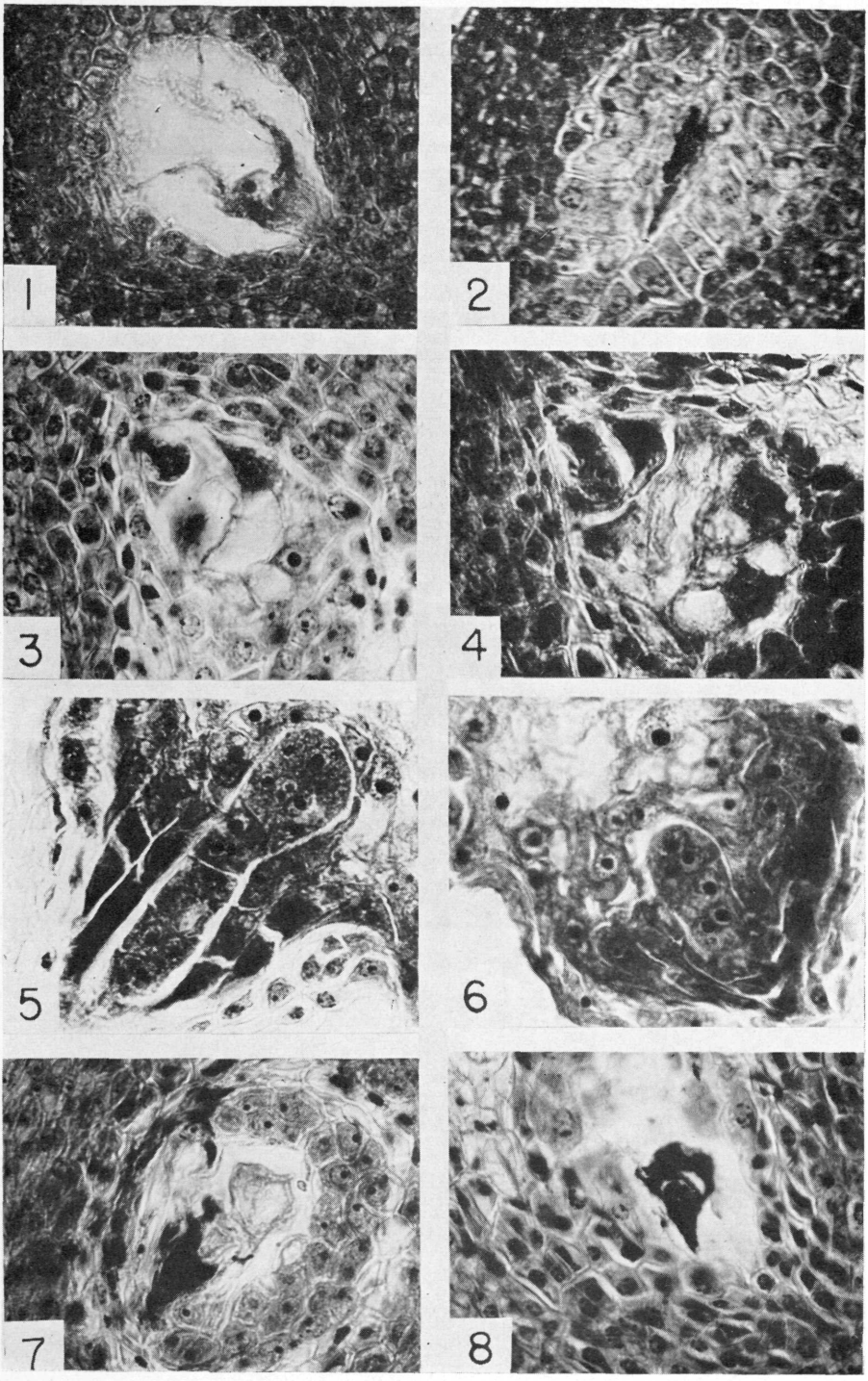
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TABLE 1

Examination of zygotes or embryos in 2347 embryo sacs of 16 fruits of woolly plants

Fruit number	Interval between pollination and removal of fruit, in hours	Stage of embryonic development*	Number of embryo sacs examined	Number of embryo sacs showing disintegration therein	Number of normal embryo sacs	Percent of embryo sacs showing disintegration therein
Class I						
49–3	131	Z.	125	22	103	17.6
16 b	139	Z.	239	35	204	14.6
16 b 4	139	Z.	173	50	123	28.8
56	141	Z.	121	42	79	34.7
20 b 2	143	Z.	186	54	132	29.3
20 b 3	143	Z.	184	28	156	15.2
Total			1028	231	797	
Mean			171±18	39±5	133±18	22.5±3.5
Class II						
49–2	131	2C, Z	100	27	73	27.0
49–4	131	2C, Z	133	28	105	20.9
50–2	139	4C, 2C, Z	142	22	120	15.5
49	131	4C, 2C, Z	120	10	110	8.3
50	139	4C, 2C, Z	80	22	58	27.5
Total			575	109	466	
Mean			115±11	22±3	93±12	19.0±3.7
Class III						
44–3	150	2C	141	33	108	23.4
40	146	2C, 4C	200	34	166	17.0
44	150	emb	95	30	65	31.6
44–2	150	emb	135	65	70	48.1
44–6	150	emb	173	39	134	22.5
Total			744	201	543	
Mean			149±18	40±6	109±19	27.0±5.4

*Z = zygote, 2C = 2-celled embryo, 4C = 4-celled embryo, emb = embryos more than 4 celled.

MATERIAL AND METHODS

1. Embryo sac study.—Woolly and nonwoolly tomato plants for this study were set in the field in the spring of 1951. All were progeny by selfing from one woolly plant. However, the plants were heterozygous for many factors such as fruit color and potato leaf. From August 30 to September 3, 1951, flowers of both woolly and nonwoolly plants were emasculated, self pollinated immediately,

EXPLANATION OF FIGURES IN PLATE II

9. Disintegrating zygote and endosperm. Synergids have also disintegrated. 461×.
10. Embryo sac with a normal zygote and disintegrating endosperm. Synergids have already disintegrated. Zygote upper right. 461×.
11. Embryo sac with beginning zygote disintegration. Normal endosperm. Zygote lower center between and above two darker stained cells. 461×.
12. Embryo sac with beginning zygote and endosperm disintegration. Zygote upper center between two other cells. 461×.
13. Embryo sac with disintegration of a four-celled embryo. These cases were rare. Normal endosperm. 461×.
14. Embryo sac with disintegration of a two-celled or larger embryo. These cases were rare. 461×.
15. P.M.C. showing possible evidence of a heterozygous deletion as indicated by arrow. Note clarity of spindle fiber attachment point in darkly stained portion near nucleolus. 1036×.
16. P.M.C. showing no evidence of a heterozygous deletion. Region where expected is indicated by arrow. This is same cell as figure 15 but at a different focal plane. 1036×.

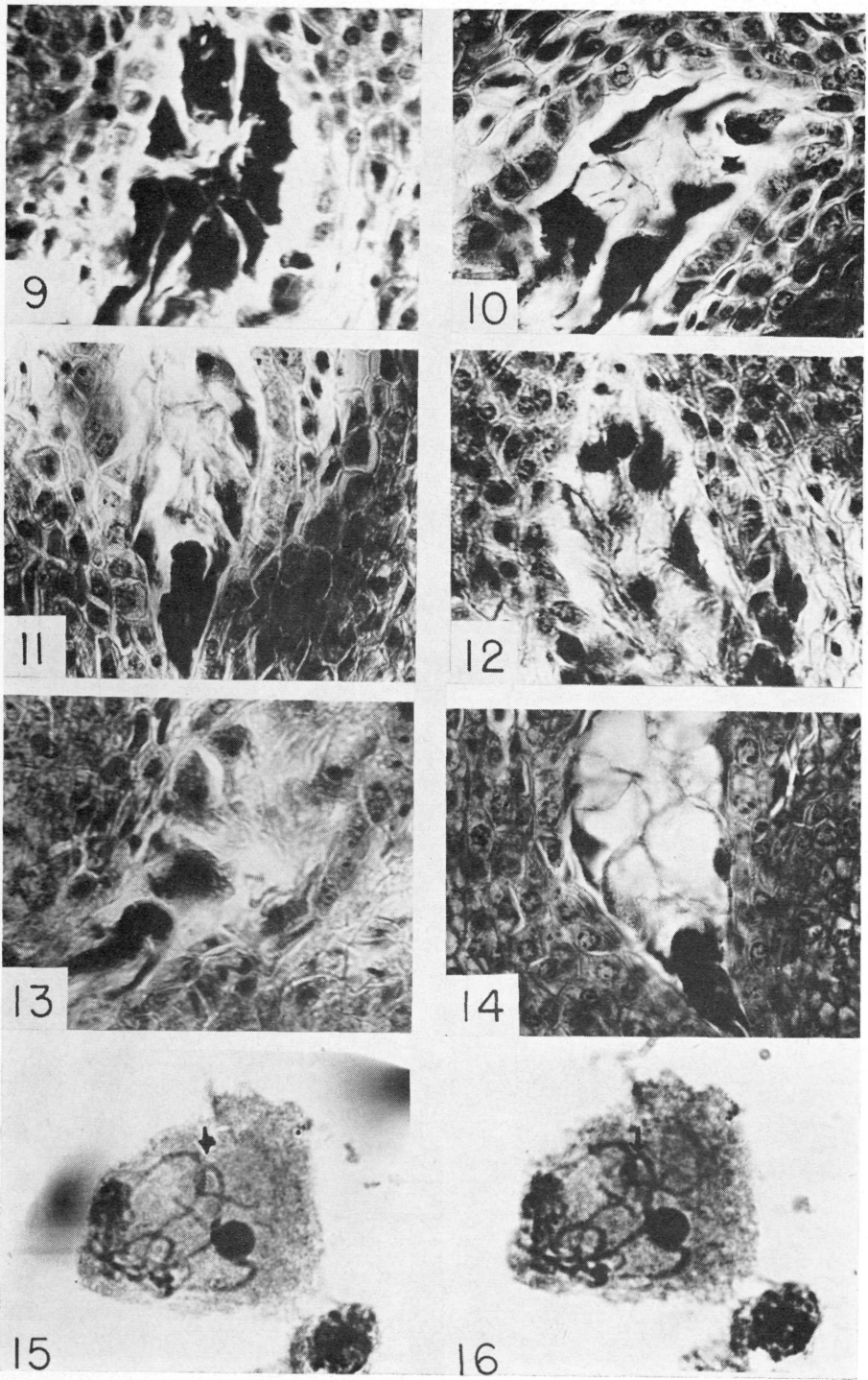
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TABLE 2

Examination of zygotes or embryos in 678 embryo sacs of 6 fruits of nonwoolly plants

Fruit number	Interval between pollination and removal of fruit, in hours	Stage of embryonic development*	Number of embryo sacs examined	Number of embryo sacs showing disintegration therein	Number of normal embryo sacs	Percent of embryo sacs showing disintegration therein
Class I						
19 b	145	Z	82	15	67	18.3
19 b 2	145	Z	90	20	70	22.2
19 b 3	145	Z	131	15	116	11.4
48	142	Z	126	35	91	27.8
22 b	119	Z	134	11	123	8.2
Total			563	96	467	
Mean			113±11	19±4	93±11	17.1±3.5
Class II						
41	150	Z, 2C, 4C	115	43	72	37.3

*Z = zygote, 2C = 2-celled embryo, 4C = 4-celled embryo.

and bagged with at least a double layer of a fine mesh cheesecloth. All unopened and small flowers were removed from the flower cluster before bagging. From September 3 to September 7, 1951, fruits of both woolly and nonwoolly plants were removed for sectioning at intervals from 80 to 150 hours after pollination.

Serial sections of the fruits were examined for zygotic and embryonic development. Embryo sacs which contained normal zygotes or embryos and endosperm (fig. 3 to 6) and those which showed disintegration of the zygote, embryo, or endosperm (fig. 2 and 7 to 14) were counted.

2. *Seed study.*—Ten fruits per plant were taken from 18 woolly plants and from ten nonwoolly plants in August, 1951. The fruits were cut open and all normal sized seeds were removed and counted.

Seeds were collected and saved from ten fruits per plant of ten woolly and ten nonwoolly plants in September, 1951. Some but not all of the fruits were from the same plants from which seed counts were taken. Seeds from each plant were composited. In December, 1951, germination tests of 50 seeds from each woolly and each nonwoolly plant were conducted on moist filter paper in Petri dishes.

3. *Examination of pollen mother cell smears.*—Acetocarmine smears of pollen mother cells from anthers of greenhouse grown woolly plants were examined for evidence of a heterozygous deletion in the pachytene stage of meiosis. Since Barton had found that the woolly locus is on the nucleolar chromsome, that chromosome was the only one examined in detail. Some cells were observed in which the nucleolus and most of the nucleolar chromosome were pushed away from the rest of the chromosomes as a result of smearing. Most of the nucleolar chromosome was thereby visible. Since in cells of this type better observations could be obtained, most attention was given to these cells (fig. 15 to 18).

4. *Description of the woolly character.*—The expression of the woolly character was studied in a field planting of tomatoes during the summer of 1951. Similar above ground parts of woolly and nonwoolly plants were compared visually. In addition comparable stems, anthers, and styles were examined microscopically and photographed. Particular attention was paid to the length of epidermal hairs on both woolly and nonwoolly plants and to the parts of woolly plants where profuse epidermal hair growth occurred to observe whether any differences exist between woolly and nonwoolly plants.

5. Hybridization with Lycopersicon hirsutum.—Pollen from a *L. hirsutum* plant was applied to emasculated flowers of woolly and nonwoolly greenhouse grown tomato plants during the early spring of 1951. Seeds from these crosses were planted the same year and the resulting plants along with some *L. hirsutum* plants were transplanted to the field. During the summer of 1951, the plants were visually observed to see whether any had both the longer epidermal hairs of *L. hirsutum* and the shorter hairs of woolly *L. esculentum*. In addition, comparable stem segments of woolly *L. esculentum*, *L. hirsutum*, and the F_1 hybrid were photographed.

RESULTS

1. Embryo sac study.—The data of tables 1 and 2 have been arranged into three classes:

Class I—those fruits with all embryo sacs containing zygotes;

Class II—those fruits with embryo sacs variously containing zygotes, two-celled, and four-celled embryos;

Class III—those fruits with embryo sacs variously containing two-celled, four-celled, and many celled embryos.

The data in tables 1 and 2 indicate significant variation among classes in the total number of embryo sacs examined per fruit, embryo sacs with disintegration, and normal embryo sacs. To control this variable, the data were converted to percent of embryo sacs having disintegration.

In comparing data from fruits of woolly plants in table 1, Class I with data from fruits of nonwoolly plants in table 2, Class I, the difference of 5.4 percent more embryo sacs with disintegration in woolly plants is statistically nonsignificant. The data from fruits of woolly plants in Class II indicate there is a decrease, although probably nonsignificant, in percent embryo sacs with disintegration compared with data from fruits of woolly plants in Class I. Comparing data from woolly fruits in Class III, there is a 4.5 percent increase in embryo sac disintegration over Class I woolly fruits, or a 10 percent increase over Class I nonwoolly fruits. This 10 percent increase is not significant so far as lethal action of the homozygous woolly character is concerned.

The data in table 1 show that the stage of development within the embryo sac was not necessarily associated with the interval of time between pollination and removal of the fruit; e.g., embryos of fruits 50–2, 49, and 50 were at a more advanced developmental stage than those of fruits 56, 20 b 2, and 20 b 3, although there was a greater time interval between pollination and removal of the fruit in the case of fruits 56, 20 b 2, and 20 b 3 than in the case of fruits 50–2, 49, and 50. However, considering the sample as a whole, there was a tendency for fruits removed 131 to 143 hours after pollination to have embryo sacs containing embryos at the zygotic, two or four celled embryonic stage, while fruits removed 146 to 150 hours after pollination tended to have embryo sacs containing embryos at the many celled embryonic stage. The flowers for this part of the investigation were not necessarily at the same stage of development when pollinated. The flowers may have been emasculated as much as a few hours to one whole day prior to the beginning of anthesis. Even if flowers had been pollinated at the same developmental stage, subsequent development would not necessarily occur at the same rate, especially between flowers of different plants. This could, at least in part, account for the fact that disintegration of the embryo was not associated with a particular lapse of time between pollination and removal of the fruit for sectioning.

The data in tables 1 and 2 do not include fruits from the entire range of sampling. Fruits with a time interval of less than 119 hours between pollination and removal of the fruit for sectioning contained primarily embryo sacs within which it is doubtful that fertilization had occurred. A few fruits with a time interval greater than 119 hours between pollination and removal of the fruit for sectioning

contained primarily embryo sacs of this same type, and hence also were not included. Since it had already been assumed that the lethal action of the homozygous woolly character occurs after fertilization, little information concerning this problem would have been gained by observing fruits with embryo sacs in which fertilization had not occurred.

Some embryo sacs were observed within which it could not be determined whether fertilization had occurred. Figure 1 is a typical embryo sac of this type containing two nuclei, one larger than the other. It could not be concluded whether the larger nucleus was the fusion nucleus or the primary endosperm nucleus. The smaller might be the nucleus of the egg cell or that of the zygote. Since it was thus impossible to determine whether fertilization had occurred, embryo sacs at this stage of development were not included in the data presented in tables 1 and 2. In the fruits, the data from which are included in tables 1 and 2, embryo sacs in which fertilization could not be recognized were found mostly at the basal end. Since fertilizations occur over a period of time, the ovules in this part of the fruit were the last to be fertilized.

The data in tables 1 and 2 include collapsed embryo sacs (fig. 2) in which it could not be ascertained whether the embryo sac collapsed prior to fertilization (and hence should not be included here) or after fertilization. A collapsed embryo sac indicates that distintegration of its components has occurred but it does not indicate at which developmental stage this disintegration occurred. A collapsed embryo sac is considered as an advanced stage of disintegration.

Figures 3 to 6 are typical examples of embryo sacs containing normal embryos. Figure 3 shows one at the zygote stage. The nucellus and possibly a small amount of the integument can be seen surrounding the embryo sac. Figure 4 shows an embryo sac containing a two-celled embryo. Several endosperm cells can be observed. Figures 5 and 6 illustrate embryo sacs containing many celled embryos.

Figures 2 and 7 to 14 are typical illustrations of disintegration within an embryo sac. Figure 2 is a collapsed embryo sac of the type previously discussed. The embryo within the embryo sac shown in figure 7 is at the zygote stage, judging by the comparative size of the embryo sac. The zygote and endosperm cannot be distinguished since both are disintegrating.

Figure 8 is similar to figure 7 although possibly the zygote is a little better defined. Both the zygote and endosperm are disintegrating. Figure 9 illustrates an embryo sac containing a zygote, which along with the endosperm is disintegrating. The zygote is probably the cell at the upper center of the embryo sac.

EXPLANATION OF FIGURES IN PLATE III

17. P.M.C. showing possible evidence of a heterozygous deletion as indicated by arrow. 1036×.
18. P.M.C. showing no evidence of a heterozygous deletion. Approximate region where expected is indicated by arrow. 1036×.
19. Style segment of woolly *L. esculentum* on the left comparible with that of nonwoolly *L. esculentum* on the right. Note that the upper portion of the style has few or no epidermal hairs in either case. Note greater profuseness of epidermal hair growth on woolly style. 15×.
20. Anther segment of woolly *L. esculentum* on the left comparable with that of nonwoolly *L. esculentum* on the right. Note that profuseness of epidermal hair growth is nearly the same in both cases. 15×.
21. Stem segment of woolly *L. esculentum*. Compare length of epidermal hairs with those in Figure 22. 15×.
22. Stem segment of *L. hirsutum*. Note length of epidermal hairs as compared with figure 21. 15×.
23. Stem segment of an F_1 plant of a woolly *L. esculentum* x *L. hirsutum* cross. This condition is here named superwoolly. Note presence of both short and long epidermal hairs. Compare with figures 21 and 22. 15×.

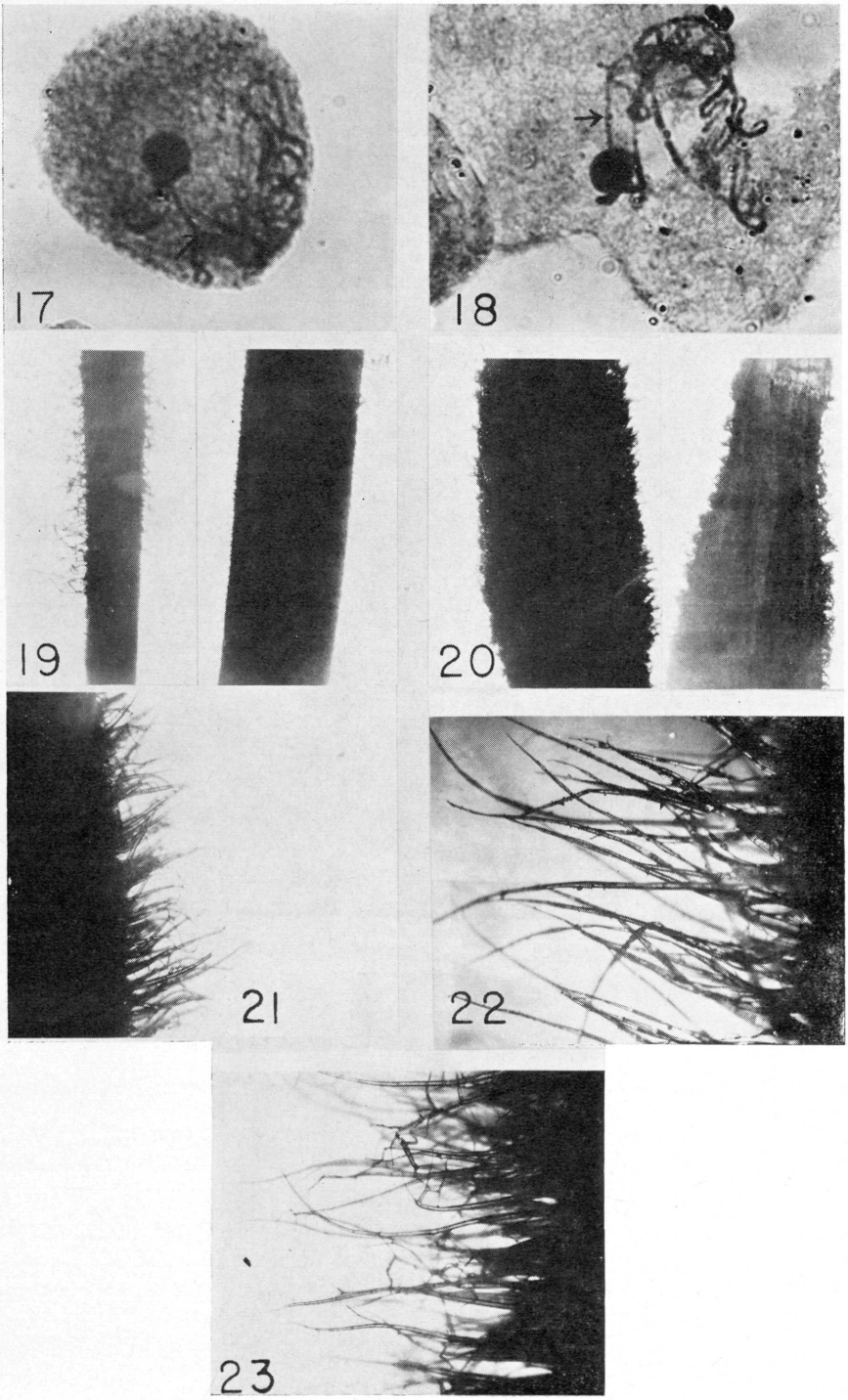
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Figure 10 shows an embryo sac containing a zygote. Several endosperm cells are disintegrating although the zygote, located at the upper right of the embryo sac, still shows a nucleolus but is probably disintegrating. In embryo sacs of nonwoolly plants, 22 such cases were observed while in embryo sacs of woolly plants only three were observed. Compared with the number of embryo sacs observed, these numbers are small. These cases were not considered in computing the amount of disintegration in tables 1 and 2 since it was not certain that the zygote was disintegrating.

Figure 11 illustrates an embryo sac containing a zygote. Endosperm cells are normal. Three other cells are to be noted at the lower center of the embryo sac of which the two darker stained cells might be disintegrating synergids and the third cell, in which the nucleolus is still evident and which is lighter stained, might be the zygote at an early stage of disintegration. Figure 12 shows an embryo sac containing a zygote between two endosperm cells at the upper center of the embryo sac. Two more endosperm cells can also be seen. All cells are at a fairly early stage of disintegration. Figure 13 illustrates an embryo sac probably containing a four-celled embryo which is disintegrating and at least five normal endosperm cells. Figure 14 shows an embryo sac containing a two-celled or larger embryo with at least two normal or nondisintegrating endosperm cells. Disintegration of embryos more advanced than the zygotic stage was rarely seen. In fact, of all the embryos observed to be disintegrating at any stage, only three were composed of two or more cells, two of which were photographed as figures 13 and 14. As is illustrated in figures 11, 13, and 14, in a number of cases in embryo sacs of both woolly and nonwoolly plants, the zygote or embryo disintegrated but the endosperm did not.

TABLE 3 (Summary of Table 6)

Number of normal sized seeds per fruit from 18 woolly and 10 nonwoolly plants, 10 fruits per plant

	Fruits from woolly plants	Fruits from nonwoolly plants
Total seeds counted	17495	9333
Mean number of seeds per fruit	97±4	93±4

2. Seed study.—The number of normal sized seeds per fruit of woolly and nonwoolly plants was nearly the same, as indicated by the data presented in table 3. The mean number of normal sized seeds per woolly fruit was 98±4 and per nonwoolly fruit was 93±4. Since analysis of variance requires the same number of entries per type of sample, data from the first ten woolly plants from which fruits were taken and data from fruits of the ten nonwoolly plants were compared. The results are presented in table 4. The F values obtained are smaller than those required for significance at the 5 percent level. Therefore, it can reasonably be stated that the difference in number of normal sized seeds per fruit from woolly and nonwoolly plants is not statistically significant.

TABLE 4

Analysis of variance of the number of normal sized seeds of 10 fruits of each of 10 woolly and 10 nonwoolly plants

Source of variation	Degrees of freedom		Sum of squares	Mean square	F	$F_{.05}$
Total		199	586655	2948.07		
Between plants	19	19	177083	9320.16	1.010	2.18
Between genotypes	1		11553	11553.00	1.256	247.00
Within genotypes	18		165530	9196.11		
Within plants		180	409582	2275.46	0.247	1.66

TABLE 5

Germination tests of 500 seeds from woolly and nonwoolly plants

Plant number*	Number of seeds germinating per 50
16W	29
17W	31
19W	30
21W	21
23W	39
24W	36
25W	31
26W	26
27W	17
29W	34
Total	294
Mean	29.4±0.68
Mean percent germination	58.8±1.35
13NW	45
15NW	48
18NW	18
19NW	36
20NW	47
22NW	45
23NW	44
25NW	18
26NW	42
32NW	45
Total	388
Mean	38.8±1.15
Mean percent germination	77.6±2.28

Number of woolly seeds expected to germinate = 313

$$\chi^2 = \frac{294-313-.5^2}{313} = 1.215$$

P = .30–.20

*W = woolly plant, NW = nonwoolly plant.

In table 5 data are presented which indicate that 18.8 percent fewer seeds germinated from woolly plants than from nonwoolly plants. Actually, the decrease in germination of seeds from woolly plants is expected to be 19.4 percent rather than 25 percent. A chi-square test of the difference between 18.8 percent and 19.4 percent gave a value of 1.215 with a probability of .30 to .20. Any extrinsic factor which causes some of the seeds from nonwoolly plants to fail to germinate would be expected to cause the same proportion of seeds from woolly plants to do likewise. Any such factor would also be expected to exert its influence independently of the lethal action of the homozygous woolly character. Therefore, some of the decrease in germination in seeds from woolly plants would presumably be due to any factor which causes seeds from nonwoolly plants to fail to germinate plus the lethal action of the homozygous woolly character operating in the same seed. This would make the decrease in germination due to lethal action of the homozygous woolly character appear less than 25 percent by an amount equal to the product of the frequency of factors operating in nonwoolly plants times the frequency of lethal action of the homozygous woolly condition. This has been taken into consideration in arriving at the number of woolly seeds expected to germinate.

3. *Examination of pollen mother cell smears.*—If a deletion were present on one

member of the nucleolar pair of chromosomes, the pachytene configuration would show a hump in one chromosome where it would have no homologous part of the deleted chromosome with which to synapse. The size of this hump would depend on the size of the deletion. If a deletion were not present, the pachytene configuration would be normal, i.e., synapsed throughout. In figure 15 some evidence of a heterozygous deletion might be seen; but in figure 16 which is a photomicrograph of the same cell at a different focal plane, no such evidence is seen. If the deletion hump occurred in a plane perpendicular to the plane being observed, the pachytene configuration would appear normal, excepting that at that point where the deletion occurred, it would appear as though there were a portion of the chromosome which did not stain. Such a configuration is possibly seen in figure 17. Although some cells were observed which show such slight or fair evidence of a heterozygous deletion, many cells were observed (e.g., fig. 18) which showed no evidence of a deletion. If a deletion were actually present, it should be demonstrable in all suitable pachytene preparations from woolly plants.

4. *Description of the woolly character.*—The woolly character was found to be expressed on most above ground plant parts which included leaves, stems, sepals, petals, parts of styles, and fruits. Below ground plant parts were not investigated. Epidermal hairs are absent from the upper one-third of the styles of both woolly and nonwoolly plants. They are present only on the basal two-thirds of the style in both and are more profuse on styles of woolly plants than on those of nonwoolly plants. Figure 19 illustrates a style segment of a woolly plant on the left and a comparable style segment of a nonwoolly plant on the right. The epidermal hair growth on anthers of woolly plants was not more profuse than that on anthers of nonwoolly plants. This is illustrated in figure 20, which shows an anther segment of a woolly plant on the left and a comparable anther segment of a nonwoolly plant on the right.

5. *Hybridization with* Lycopersicon hirsutum.—F_1 plants of a species cross involving *L. hirsutum* and woolly *L. esculentum* have both the longer epidermal hairs of *L. hirsutum* and also the shorter epidermal hairs of woolly *L. esculentum*. It is here proposed to designate formally this composite characteristic "superwoolly." Figure 21 illustrates epidermal hairs on a stem of woolly *L. esculentum*. Figure 22 shows epidermal hairs on a *L. hirsutum* stem. From this comparison it may be seen that woolly *L. esculentum* stems had much shorter epidermal hairs than *L. hirsutum* stems. In figure 23, which is from an F_1 plant of a woolly *L. esculentum* x *L. hirsutum* cross, it can be seen that this hybrid had the superwoolly condition. This superwoolly condition occurred on most above ground parts. This indicates that epidermal hair growth of these two species is governed by different genes. Other morphological characters of these F_1 hybrids more nearly resembled *L. hirsutum* than *L. esculentum*.

DISCUSSION

1. *Embryo sac study.*—No evidence of lethal action of the homozygous woolly character was found within the time range of early embryonic development sampled in this investigation. The only irregularity in development studied here was embryo sac disintegration. Other irregularities may occur at other developmental stages of the embryo, and there may be differential growth rates of woolly and nonwoolly embryos. It is possible that embryos might develop to a certain stage and subsequent development cease as a result of lethal action, which would result in seeds containing poorly developed embryos incapable of germination.

Since, in observing collapsed embryo sacs, it could not be ascertained whether fertilization had occurred, an unavoidable error may have been introduced. However, the number of collapsed embryo sacs which occurred before fertilization would be expected to be the same in both cases. For that reason, the comparison of the amount of disintegration of embryo sacs after fertilization in woolly and non-

TABLE 6

Number of normal sized seeds per fruit from 18 woolly and from 10 nonwoolly plants

Plant number*	Fruit number 1	2	3	4	5	6	7	8	9	10	Total
21W	153	138	128	140	62	14	169	140	69	156	1159
22W	119	129	122	109	38	48	59	30	92	90	836
23W	52	19	100	133	166	106	138	103	143	125	1085
24W	281	17	220	26	170	200	146	147	178	126	1511
25W	88	9	31	34	29	136	127	161	130	185	930
26W	128	135	196	77	157	161	178	142	153	170	1497
27W	134	123	88	112	148	81	136	132	81	119	1154
28W	40	95	92	34	66	100	102	55	37	60	681
32W	115	143	125	18	88	18	134	19	74	97	831
33W	172	74	114	164	142	39	94	165	66	139	1169
34W	54	109	117	28	62	64	27	57	154	130	802
35W	72	39	83	75	113	105	177	43	157	110	974
36W	68	175	43	134	107	87	49	71	70	113	917
38W	66	138	134	56	104	91	107	105	33	145	979
39W	26	164	31	37	60	50	43	77	80	51	649
43W	150	89	107	58	122	107	99	154	115	119	1120
44W	84	60	70	18	53	37	64	81	92	35	594
45W	44	158	76	61	44	37	71	51	57	8	607
Total											17495
Mean											97±4
14NW	37	120	42	37	68	29	54	30	61	45	523
15NW	127	163	37	117	78	60	121	68	100	35	906
16NW	171	194	144	160	111	143	214	127	126	147	1537
17NW	195	125	106	112	129	138	137	98	130	99	1269
18NW	131	80	56	121	53	111	46	126	36	133	893
20NW	103	65	35	76	30	12	35	78	87	85	606
22NW	86	81	20	40	54	92	89	65	110	104	741
23NW	109	12	14	18	124	113	120	102	22	68	702
25NW	20	210	195	21	189	48	136	181	261	24	1285
26NW	47	62	133	81	164	49	85	122	113	15	871
Total											9333
Mean											93±4

*W = woolly plant, NW = nonwoolly plant.

woolly plants would be expected to be a valid approach to the question being considered.

If the cases where endosperm only and neither the zygote nor embryo disintegrated were due to an action of the homozygous woolly gene, one would expect to observe fewer such cases in embryo sacs of nonwoolly plants than in those of woolly plants. The fact is that more were observed and for this reason it was considered permissible to exclude such cases from the data presented.

In a few embryo sacs of both woolly and nonwoolly plants the zygote disintegrated and the endosperm did not. Several factors could account for the zygote disintegration without endosperm doing likewise: *1.* There could be some differential effect of environmental conditions on the embryo and endosperm. *2.* The endosperm might have disintegrated subsequent to the stage observed here. *3.* The triploid endosperm genotype might have been viable even though the diploid zygote genotype was inviable.

2. Seed study.—In view of the significant reduction in germination found in seeds from woolly fruits, lethal action of the homozygous woolly condition must have occurred prior to seed maturity, a mature seed being considered as one capable of germination. Therefore, the lethal action evidently occurred between the many celled embryo stage studied here and seed maturity. It might be pos-

sible that, if lethal action occurred early in the development of the embryo, the endosperm and integument might continue normal development, resulting in normal sized seeds with little or no embryo. However, it seems more plausible that, if lethal action occurred early in embryo development, the endosperm and integument sooner or later might also be affected, thereby resulting in smaller seeds. If this were the case and normal sized seeds of woolly and nonwoolly plants were counted, the number per fruit on an average should be significantly different. This, however, was not observed; and, therefore, it seems reasonable to assume that the lethal action occurred later in embryonic development. If the few plants Soost suspected of being homozygous woolly were actually that, it would indicate that lethal action of this homozygous woolly character occurred late enough in development that the embryos which occasionally escaped this lethal action were then able to germinate. If this is the case, it seems reasonable to say that lethal action of the homozygous woolly character probably occurs shortly before seed maturity.

3. *Examination of pollen mother cell smears.*—On the basis of evidence presented, it is doubtful whether the woolly character is due to a deletion unless the deletion is quite small. However, if the woolly character is due to a deletion, then the expression of woolliness is correlated with the absence of a gene rather than the presence of one.

4. *Description of the woolly character.*—Since epidermal hair growth was found to be more profuse on leaves, stems, sepals, petals, basal two-thirds of the length of styles, and fruits of woolly plants than on those structures of nonwoolly plants, the expression of the woolly character is thus not limited to vegetative parts although it is not always evident on all reproductive plant parts.

5. *Hybridization with* Lycopersicon hirsutum.—The production of superwoolly plants revealed that the genes are different. Whether or not they are alleles is not yet determined. If they are alleles, then neither one is dominant to the other.

SUMMARY

1. No lethal action of the homozygous woolly condition was observed from the zygote stage to the twenty- to thirty-celled embryo stage.

2. The average number of normal sized seeds per mature fruit of woolly plants was very close to that of nonwoolly plants.

3. The average germination of seeds of woolly plants was 25 percent less than that of seeds of nonwoolly plants. This was a significant difference.

4. The lethal action of the homozygous woolly condition probably takes place shortly before seed maturity.

5. It is doubtful that a chromosomal deletion is the cause of the woolly character.

6. The woolly character appears on at least some reproductive parts as well as on vegetative parts.

7. Superwoolly tomato plants were produced by crossing *L. hirsutum* with woolly *L. esculentum*. Hence, epidermal hair growth of these two species must be governed by different genes. If allelic, these genes lack dominance.

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